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SHORTER ARTICLES AND DISCUSSION

THE INHERITANCE OF SEASONAL POLYMORPHISM IN BUTTERFLIES

ARE seasonal variations inherited, and may they play a part in evolutionary change? These are questions which Punnett in his recent book on "Mimicry in Butterflies" answers in the negative.

> In no case are they known to be inherited, and in no case consequently could variation of this nature play any part in evolutionary change.

Variations to be of significance in evolution, he tells us, must be "transmissible and independent of climatic and other conditions."[1]

It would seem to require no demonstration that well-established seasonal variations like those of *Araschnia levana-prorsa* of Europe in which, it will be remembered, the ground color of the spring brood (*levana*) is red-brown, that of the summer brood (*prorsa*) black, are transmissible. Under summer conditions in Europe *prorsa* appears with the regularity of a monotypic species, true to type. Monotypic species likewise require a certain degree of temperature and amount of moisture to produce their characteristic adult coloration. *A. prorsa* is by no means peculiar in this respect. It has the definitive adult coloration of the species. That which is peculiar is the hereditary rhythmic tendency to swing from *prorsa* back to *levana*, which is so strong that experimental control can not wholly cope with it. Summer conditions artificially prolonged result in the appearance of some *prorsa* in *prorsa's* immediate offspring, but sometimes the intermediate, *porima*, is the outcome. A far larger number of individuals of the lot under experimentation, however, refuse to be forced out of the chrysalis by artificial heat, hibernate, and become *levana*. These color variations, therefore, are not subject wholly to the environment, nor wholly to heredity.

A common hereditary basis evidently underlies both of the color patterns. Like produces like, but under natural conditions only by skipping a generation. Except for the innate tendency for the types to alternate, the case is similar to that of the red primrose described by Baur[2] which, growing at 15°–20° C. produces red flowers, at 30°–35° C., white. Or it is like the mutant stock of *Drosophila* described by Miss Hoge,[3] which, bred in winter or in an ice chest, gives a large proportion of flies with supernumerary legs, though in summer or in moderate temperature the stock appears to be normal. The same set of factors under varying conditions produces different results. An analysis of the factors underlying another similar case in *Drosophila*, "abnormal abdomen," has been worked out by Morgan.[4] This remarkable mutant was shown to behave as a dominant sex-linked character. It manifests itself, however, only when the food in which the flies are bred is kept moist.

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[1] Pp. 131, 132.

The rhythmic tendency of *prorsa* to produce *levana*, notwithstanding artificial raising of the temperature, shows that this is a sort of alternation of generations in which the definitive sexual generation, *prorsa*, alternates with another apparently more primitive, *levana*, which is also sexual. This seasonal alternation of sexual forms in its hereditary basis is comparable to typical alternation of asexual and sexual types.

Weismann,[5] in discussing the case cited, assumed the presence simultaneously in the germ plasm of *prorsa*-determinants and *levana*-determinants.

> But these *prorsa*-ids were at the same time so arranged that they became active under the action of a higher temperature, if this is acting at the beginning of the pupal period, while the *levana*-ids become active at a lower temperature. Heat, therefore, is only the excitant which sets free the *prorsa*-determinants, while cold sets free the *levana*-determinants.

Modernizing Weismann's hypothesis, may we suppose that distinct Mendelian factors underlie each of these two discontinuous types of coloration? The idea is attractive, but all the evidence at hand indicates that the determinants or factors of both types are borne by all the gametes. Intermediates, showing a combination of the two patterns, called *porima,* occur under certain temperature conditions. The two patterns can not be Mendelian allelomorphs of each other, though the possibility remains they may have undiscovered allelomorphs. Too little is now known of inheritance in this species for us to judge whether Weismann's hypothesis in modern form is tenable, or whether a single set of factors, or single factor, reacting differently to different environments, is sufficient to account for the two types.

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[2] "Einführung in die Vererbungslehre," pp. 4–6.

[3] *Jour. Exper. Zool.*, 18, 1915.

[4] "Mechanism of Mendelian Heredity," pp. 39–41.

[5] "New Experiments on the Seasonal Dimorphism of Lepidoptera." Translation by Nicholson in the *Entomologist*, 1896.

In a preliminary analysis of the problem the two color phases seem like distinct ontogenetic stages. *Levana* possibly is *prorsa* with immature colors, arrested in their development through the action of cold. *Prorsa* in the chrysalis may pass rapidly through the *levana* stage into its final, complete condition. Its offspring, however, independently of the environment, hereditarily tend to hibernate in the chrysalis and become *levana.* This interpretation of the two color phases is in line with the facts of dichromatism in beetles, as described by McCracken[6] and others. *Gastroidea dissimilis,* when it emerges from the pupal case, is black, and certain individuals permanently retain this color, others, however, pass on to a permanent bright green phase. *Lina lapponica* (*Melosoma scripta*) has a spotted-brown phase which is either permanent or is replaced by black. The two color phases in each of these forms, however, are Mendelian allelomorphs of each other, the dominant color being that appearing first in ontogeny, the recessive last.

The cold weather varieties of *Colias eurytheme,* about to be discussed, certainly may be regarded as being produced in large part by the arrested development of pigmentation. In this most remarkable seasonally polymorphic butterfly of western and central North America, *Colias eurytheme,* the writer has found that the flaming orange coloration of the summer form (usually called the typical *eurytheme*) and the paler orange-yellow of the spring and autumn broods (*ariadne* and *keewaydin*) are variations also due to differences in the reaction to the environment of definite Mendelian factors. This has been shown by crossing the orange *eurytheme* of the central and western states, with the clear yellow species of the eastern and central states, *Colias philodice,* the yellow of which segregates cleanly from the orange in F_2, as a recessive. The hybrids, as well as the *eurytheme* stock, show seasonal polymorphism. The F_1 hybrids, for example, are of a dilute orange. Orange is therefore incompletely dominant. The heterozygote is an intermediate. The amount of orange pigmentation, or the degree of its dilution, in the F_1 hybrids, however, varies prodigiously with the season. The summer-bred hybrid is of dilute orange (''apricot yellow'') somewhat evenly distributed over the wings, but in the small winter-bred individuals, such as emerge in the greenhouse in December, the orange is restricted to a faint flush near the posterior (inner) margin of the fore wings.

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[6] *Jour. Exper. Zool.,* 3, 1906.

But even though the underlying hereditary basis supports a superstructure that varies widely, are these variations *as such* inherited? The variety of *eurytheme* called *ariadne* is small and of a pale orange hue. This form appears under cold weather conditions only. Its dwarfness is due to the failure of the caterpillar to feed during the late fall to full size, though food is abundantly supplied. The shortness of the day evidently is a factor in checking the feeding. The caterpillar forages actively at mid-day, but becomes sluggish before nightfall, yet it matures even while it is not feeding, and hence produces a dwarfed pupa. The pale color may be readily explained by the supposition that the elaboration of chromogenic substances in the blood of the pupa is checked by the cold so that these materials ripen in the scales of the wings merely into faint orange and yellow.

Ariadne's progeny in June are not *ariadne,* but a large and brilliantly orange insect. Are *ariadne's* size and hue, therefore, not inheritable, but dependent wholly upon the environment? At first thought this would seem to be the fact, and this was evidently the view of the matter presenting itself to Punnett when he stated that such variations are not inherited. We have seen, however, that they are hereditary in the sense that this organism must react in this particular way under these particular conditions. Its inherited organization compels, determines, this reaction.

These seasonal variations are therefore transmissible, though they are by no means ''independent of climatic and other conditions.'' May they, therefore, play no part in evolutionary change? We should not yet be dogmatic as to this. The underlying hereditary basis in all probability is as susceptible to mutation, to disturbances in the arrangement and nature of the chromosomal elements, as any other germ-plasm. It would seem by no means impossible that the alternating phenotypes of *A.*

levana-prorsa, for example, might in suitable diverse climates, subarctic and tropical, respectively, be fixed as separate species.

A. levana bred in Labrador, for example, where it could produce only one brood, probably would not show its *prorsa*-producing tendency at all. This supposition is confirmed by Trybom's observation (quoted by Weismann) that in Siberia, where a single brood occurs yearly, it is *levana only.* Conversely, *prorsa* in the tropics would perhaps eliminate all traces of *levana,* though of this we can not be so confident.

How much practically identical germ-plasm in different parts of the world is masquerading as different species, because of the diverse ways in which it reacts to different environments in which it happens to be placed, has not been adequately investigated. An interesting example of the sort among tropical reef fishes was recently cited by Longley.[7]

> *Bodianus fulvus* and *B. punctatus* are two color phases of one species of which one may almost instantaneously replace the other.

The rapid interchange of reproductive habits between *Salamandra maculosa* and the alpine *atra* when transferred respectively to lowland or highland conditions, as described by Kammerer,[8] is probably also a case in point, due to fundamentally similar germ-plasm in both forms. Such an assumption would account for the inheritance of these readily acquired characters. If the facts are correct, *S. maculosa,* by cold and drought, was forced to assume the reproductive habits of the salamander of the neighboring alpine regions named *atra,* producing two adult larvæ viviparously, rather than many (14–72) immature embryos laid in water as is its habit in the warm, moist lowlands. Conversely, the alpine form was forced by heat and an ample water supply to increase its fecundity from two to nine larvæ at a birth. In both cases the "acquired characters" were inherited, as we would expect them to be if the two kinds of salamanders, as regards reproductive mechanism at least, have an identical or similar genotype. The fact that the lowland form living at higher altitudes has fewer young, and that the alpine form in the lower regions of its range produces an abnormally large number (viz., four) also points to the same conclusion.

It is a possibility worth considering that somatic modification accompanied by little germinal change may partially explain the remarkable "mimicry-rings" of South America that have been so interestingly discussed by Punnett. In each of several great regions of that continent a characteristic color pattern is exhibited by unrelated species belonging to different genera and even to different families. The color pattern followed in Central America differs slightly from that adopted by members of the same genera in eastern Brazil, a single genus of Pierids only dropping out of the ring in the latter region. In western Brazil and the upper Amazons the pattern is somewhat more mottled and the ground color darker, but the same genera are represented almost without exception. Finally, in Ecuador, Peru and Bolivia the pattern common to the different genera is still darker and greatly simplified. The Pierids here have left the ring, and a *Papilio*, an *Acræa* and two species of the Satyrid genus *Pedaliodes* have entered it. The point to be emphasized, however, is that the same genera, *e. g.*, *Heliconius, Mechanitis,* have representatives in each local color group.

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[7] Carnegie Institution of Washington, Year Book, No. 14, 1915, p. 209.

[8] *Archiv f. Entwicklungsmechanik,* 25, 1907.

Let us now assume, with Punnett, that a set of similar or identical color factors is common to all the structurally diverse members of each ring, and add the further hypothesis that the color pattern resulting from these particular factors is to a large extent influenced by climatic conditions, as in seasonally polymorphic insects. It then follows that certain members of a "ring" migrating from the tropical climate of Brazil to the temperate zone farther south, even before they should become changed genotypically, would react to the new environment by assuming a new color pattern such as that now characteristic of the south temperate zone. If the genotype were identical throughout the migrating group and a single member of the group should so react, all naturally would respond in the same manner. Seasonal polymorphism thus may furnish an additional clue to the explanation of this most interesting case of convergence and parallelism in evolution.

This discussion leads to the conclusion that seasonal variations have a hereditary basis more sensitive than that of other color characters to temperature and other climatic conditions. A seasonal variation that is constant in its recurrence is transmissible. Its hereditary basis invariably reacts in a certain definite way to a certain narrow range of external conditions, whereas the hereditary basis of other characters, *e. g.*, eye color in vertebrates, reacts in a precise way to a far wider range of external conditions.

Seasonal variations, as was pointed out by Weismann, show a hereditary tendency to alternate which, in some cases, is independent of external conditions.

Seasonal varieties are in some cases (*e. g., Colias,* and possibly *Araschnia*) to be regarded as distinct ontogenetic stages. Cold arrests development at an early phase in color metabolism, and the mature insect emerges with pale colors (*Colias eurytheme* var. *ariadne*), or with a color pattern different from the definitive coloration of the species (*Araschnia levana*).

The suggestion is made that local color varieties, passing it may be for distinct species, are probably in some cases the equivalents of seasonal variations. That is, they are the product of a genotype sensitive to environmental changes expressing itself under a particular set of local climatic conditions; elsewhere the same genotype may respond quite differently. Such phenomena, though not of profound evolutionary significance, may play a rather conspicuous rôle in the evolution and diversification of the colors of animals and plants.

JOHN H. GEROULD

VARIATIONS IN THE VERMILION-SPOTTED NEWT, D. VIRIDESCENS

WHILE carrying on some experiments with the spotted newt, *Diemyctylus viridescens,* I was struck with the variation in the size, number and arrangement of the black-bordered vermilion spots so characteristic of this beautiful little salamander.

It is now generally recognized that this species exhibits two phases which were formerly described as distinct varieties or even species. As described by Gage[1] the young animal, which is terrestrial in habits, is red in color and was formerly called *D. miniatus;* later it becomes aquatic and its ground-color becomes olivaceous—permanently so, according to Gage. Against this dark ground-color (which is subject to considerable variation under different conditions even in the same individual) the bright red spots with their black borders stand out very strikingly.

It was with the olivaceous phase that I was experimenting, and it is upon this phase that the following observations are based.

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[1] Gage, S. H., "The Life-History of the Vermilion-Spotted Newt," AMER. NAT., December, 1891, pp. 1084–1103.